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Eye size and acuity as selective determinants of vestibular sensitivity

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Eye size and acuity as selective determinants of vestibular sensitivity

by

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Dedication

To my parents, for finding me a place where I could learn to love learning.

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Abstract

Eye size and acuity as selective determinants of vestibular sensitivity

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The semicircular canals detect head rotations and trigger compensatory movements that stabilize gaze and help maintain visual fixation. Mammals with large eyes and high visual acuity presumably require more precise gaze stabilization mechanisms because they experience degradation of spatial resolution at a lower threshold of uncompensated motion. Because semicircular canal radius of curvature is a primary determinant of canal sensitivity, species with large canal radii are expected to be capable of more precise gaze stabilization than species with small canal radii. Here we examine the relationship between semicircular canal radius of curvature, eye size, and visual acuity in a large sample of therian mammals. Our results demonstrate that eye size and visual acuity both explain a significant proportion of the variance in mean canal radius of curvature after statistically controlling for the effects of body mass and phylogeny. These findings suggest that interspecific variation in semicircular canal radius of curvature is partly the result of selection for improved gaze stabilization in species with large eyes and acute vision.

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Introduction

The ability of the mammalian retina to sample a well focused and undistorted image is dependent both on the eye's optical features and an animal's ability to stabilize an image on the retina. Any uncompensated movements of the head that prevent an animal from maintaining visual fixation will necessarily impair visual functionality [1-3]. Mammals largely solve this problem of image stabilization by producing reflexive compensatory movements of the eyes in response to head movements (i.e., the vestibulo-ocular reflex) and of the head in response to body movements (i.e., the vestibulocollic reflex [2-4]). The importance of maintaining visual stability in species with image-forming eyes is underscored by the convergent evolution of similar mechanisms of gaze stabilization in vertebrates, arthropods, and cephalopods [2,3,5,6].

Loss of visual function due to uncompensated head movements is expected to be more problematic for species with high visual acuity and/or large eyes. Species adapted for high visual acuity tend to have smaller retinal ganglion cell receptive field centers as an adaptation for improving spatial resolution [7,8] [1]. Small, uncorrected movements of the retinal image that might degrade spatial resolution in species with small ganglion cell receptive field centers could in theory remain undetected by species with relatively large receptive field centers. Furthermore, if eye morphology is held constant, uncorrected head movements should produce absolutely greater displacements of the retinal image in

[1] Here we refer specifically to retinal circuits optimized for high acuity (e.g., the midget pathway in primates and the X/beta pathway in carnivores) rather than to higher-summation pathways mediated by ganglion cells with larger receptive fields (e.g., parasol cells).

species with large eyes compared to species with smaller eyes (Figure 1). As a result, larger and more acute eyes are expected to experience diminished visual functionality at lower thresholds of uncompensated motion than absolutely smaller eyes. Species with absolutely large eyes and acute vision are therefore also expected to require more precise mechanisms of gaze stabilization than species with small eyes and low acuity [2]. Anecdotal evidence supports the hypothesis that animals with higher acuity stabilize their gaze more precisely and permit less motion of images across photoreceptors than those with lower acuity [3,9]. Nonetheless, the relationship between eye size, visual acuity, and gaze stabilization has never been quantitatively tested using comparative data.

In mammals, the ability to sense head rotations and produce compensatory responses that stabilize gaze is mediated by the semicircular canals of the inner ear. These toroidal bony ducts in the temporal bone contain membranous endolymph-filled channels that are continuous with the utricle. As the head rotates, endolymph in one or more of the semicircular canals flows due to intertia, leading to deformation of sensory hair cells in the vestibular end-organ (crista) located at the base of each semicircular duct. These hair cells in turn modulate the firing rates of afferent vestibular neurons. These afferent signals from the six semicircular canals are integrated with visual and proprioceptive inputs to elicit the gaze stabilizing vestibulo-ocular and vestibulocollic reflexes [4,10,11]. These reflex pathways produce compensatory movements of the eye and neck that are opposite to the direction of head motion and thus help to maintain visual fixation [2,4,11,12].

Among mammals, the sensitivity of the vestibular system in detecting head rotations is strongly influenced by semicircular canal size. As the radius of curvature of a semicircular canal increases, the sensitivity of the canal to angular accelerations also increases [13-18]. As a result, species with absolutely large canal radii of curvature should be able to detect and compensate smaller head rotations than species with absolutely small semicircular canal radii of curvature. Given the need for precise gaze stabilization in species with large eyes and high visual acuity, we therefore expect eye axial diameter (AD) and visual acuity to be positively correlated with mean semicircular canal radius of curvature (R). Here we test this hypothesis through a phylogenetically controlled analysis of R, AD, and acuity in a large comparative sample of mammals. In so doing, we seek to better understand (1) the selective factors influencing the evolution of more precise mechanisms of gaze stabilization in mammals and (2) the causes of interspecific variation in R.

Methods

SAMPLE

The sample used here includes data for 111 species representing 16 mammalian orders (Figure 2). Most of the data were collected from published literature (Table 1). Data on mean R and 'agility category' for 109 species were taken from Spoor *et al* [19]. We also measured R for two additional species using methods comparable to those of [19]. High resolution CT scans of *Hemicentetes semispinosus* (AMNH 100837; in-plane resolution = 66.9μ; slice thickness = 66.9μ) and *Caenolestes fuliginosus* (KU 124015; in-plane resolution = 30μ; slice thickness = 30μ) were imported into VGStudioMax (Version 2.0; Volume Graphics GmbH, 2007). Image stacks were thresholded and resliced along the plane of each of the three canals. The height and width of each canal was then measured and R was calculated for individual canals using the formula: *canal radius of curvature* = 0.5 × (height + width)/2 [19]. Measurements of R for the anterior, posterior, and lateral canals of a single ear were then averaged.

Body mass data were taken from Smith [20] for primates and from Silva & Downing [21] for non-primate mammals. Axial eye diameter (AD), the distance between the anterior-most point of the cornea and the posterior-most point of the sclera, were taken from Ross & Kirk [22] for primates and dermopterans and Ritland [23] for all other species. Measurements of visual acuity for 33 species based on both anatomical and behavioral measurements were taken from various published sources ([24-46];Table 1).

Data on activity pattern were taken from Kirk [47]. For 20 species, diet was categorized as either 'active predator' or 'herbivore' based on Nowak [48] and Evans *et al* [49]. These categorizations were conservative and only applied if a species is either a non-scavenging hypercarnivore or a strict herbivore. Cetaceans and chiropterans were excluded from our analyses due to their derived vestibular anatomy [50,51]. Microphthalmic taxa were also excluded from the main analyses because of their highly reduced visual anatomy. However, 7 microphthalmic rodent, eulyptophitan, and marsupial species were included in a separate analysis to examine the effect of extreme eye size reduction on semicircular canal size.

ANALYSES

We used multiple statistical methods to evaluate the relationship between eye size, visual acuity and semicircular canal size. All analyses were conducted in R using the caper, geiger, nlme, and robustbase packages [52-56]. All continuous variables were log10-transformed prior to analysis. First, we assessed the independent bivariate relationships between R and both AD and visual acuity using Spearman rank correlations, ordinary least-squares (OLS) regressions, and phylogenetic generalized least-squares (PGLS) regressions. Because body mass (BM) is correlated with R, AD, and visual acuity [17,22,27,47], we also evaluated the relationships between BM and these three variables using Spearman rank correlations, ordinary least-squares (OLS) regressions, and phylogenetic generalized least-squares (PGLS) regressions. For all PGLS regressions, we estimated the degree to which the relationship between variables could be explained by a

Brownian motion model of evolution using Pagel's lambda (λ) [57]. Likelihood ratio tests were used to compare our estimate of λ to both 0 (representing no influence of phylogeny on trait distribution) and 1 (representing perfect correlation of the data with phylogeny according to a Brownian motion model). Tree topology and branch lengths in our PGLS analyses (Figure 2) follow Bininda-Emonds *et al* [58].

To examine the influence of multiple predictor variables on R, we also conducted a series of PGLS multiple regressions. These regressions include all possible combinations of BM, AD, and visual acuity as predictors of R (Table 3). Each of these models was calculated with and without interaction terms. Interaction terms that were significant in models with 2 predictor variables were included in a version of the model with all three predictor variables to determine if interaction terms remained significant. To make models comparable, the sample used in each multiple regression was limited to the 33 species for which data are available for all three predictor variables (Figure 2b). Models were compared using AICc values, which compensate for relatively small sample sizes better than standard AIC values, and better fit is indicated by lower AICc values [59].

In addition to controlling for body mass by including it as a predictor variable in our multiple regression models, we also calculated partial regressions which modeled the relationship between R and eye size or visual acuity when body mass is held constant. Bivariate PGLS regressions of all three variables of interest (AD, visual acuity, and R) against body mass were calculated to obtain residuals (AD_{res}, $acuity_{res,}$ and R_{res}). These

residuals were used to calculate PGLS partial regressions (R_{res} vs AD_{res} and R_{res} vs $acuity_{res}$).

Diet and activity pattern have both been shown to influence eye morphology [22,47,60-70] and locomotor agility has been suggested to influence R relative to body mass[19]. To determine whether these variables influence the observed relationship between R, BM, AD, and visual acuity, we included agility category [19] and activity pattern as co-predictor variables in separate iterations of the best-fit PGLS model for continuous data[2]. Because few species in our comparative sample have data for both visual acuity and dietary category, we also examined dietary category, BM, and R as co-predictors of R. All multivariate PGLS model iterations are listed in Table 3 and Table 4. As with other model comparisons, goodness of fit for alternative models was assessed using AICc values, and the contribution of individual predictor variables was evaluated using p-values and partial r^2 values. Additionally, Kruskal-Wallis tests were used to determine whether R_{res} differs according to activity pattern, agility category, or diet category. One set of tests was conducted using residuals of the overall best fit model, representing the variation in R not explained by BM, AD, and visual acuity. A second set of tests was run using the residuals of the two-predictor best-fit model, representing the variation in R not explained by BM and AD.

To examine the relationship between eye size and R in microphthalmic taxa, we included both microphthalmic (n = 7 species) and non-microphthalmic species (n = 104 species) in a bivariate plot of R on AD. A PGLS regression line was fit to non-

[2] This model has BM, AD, and visual acuity as co-predictors of R; see Results.

microphthalmic taxa and residuals were then calculated for the total sample of 111 species. The residuals of the microphthalmic and non-microphthalmic species were compared using a one-tailed Wilcoxon rank-sum test.

Results

A significant portion of the interspecific variation in semicircular canal R may be explained by variation in both eye size and visual acuity. The bivariate nonparametric correlations, OLS regressions, and PGLS regressions of R vs AD and R vs visual acuity are highly statistically significant (Table 2; Figure 3). In bivariate regression models, AD can explain 58-72% of the variance in R and visual acuity can explain 30-34% of the variance in R. The correlations between R and both AD ($\varrho = 0.83$) and visual acuity ($\varrho = 0.64$) are positive, indicating that canal radius of curvature tends in increase as both eye size and visual acuity increase in our comparative sample. However, the independent relationships between all three of these variables and BM are also highly statistically significant (Table 2; Figure 4). The correlation with BM is highest for R ($\varrho = 0.90$) and AD ($\varrho = 0.79$) but somewhat lower for visual acuity ($\varrho = 0.52$). Bivariate regression models indicate that BM can explain 76-81% of the variance in R, 53-65% of the variance in AD, and 13-25% of the variance in visual acuity. These results show that R, AD, and visual acuity all tend in increase with BM, and therefore BM is a potentially confounding variable in the observed bivariate relationships between R and AD and between R and visual acuity. Furthermore, in all bivariate PGLS regressions, Pagel's λ is ~ 0.9 or greater, revealing a substantial influence of phylogeny on the bivariate distribution of taxa (Table 2). Nonetheless, likelihood ratio tests demonstrate that Pagel's λ is also significantly different from 1.0 in these PGLS models, indicating that the relationships between AD, visual acuity, and R in OLS regressions cannot be attributed entirely to the effects of phylogeny.

In PGLS multiple regressions, all models with 2 predictor variables were statistically significant ($P < 0.001$), and both predictor variables in each model explained a significant proportion of the variance in R (Table 3). Of these regressions, the model including BM and AD most accurately predicted R, with the lowest AICc value (-97.06) and highest r^2 value (0.873) of the two-predictor models. However, the PGLS multiple regression model including all three continuous predictor variables (BM, AD and visual acuity) explained a larger amount of the variance in R ($r^2 = 0.89$) and had a lower AICc value (-99.091) than any model with 2 predictor variables (Table 3). All three predictor variables were significant in this model, with BM, AD, and visual acuity respectively explaining 59%, 24%, and 11% of the variance in R. Inclusion of interaction terms never improved the AIC values of the multiple regression models, and the only interaction term from the two-predictor models to reach significance was the interaction of BM and AD (Table 4). When this interaction term was included in the best-fit model with three continuous predictor variables, the interaction was non-significant and AICc value of the model increased substantially (Table 4). Likelihood ratio tests demonstrate that Pagel's λ values for all PGLS multiple regression models (range = 0.56-0.83; Table 3) were significantly different from both 0 and 1.

Eye size and acuity are also significantly positively correlated with R when the effect of body mass is held constant using partial correlations (Figure 5). AD_{res} explains 34% of the variance in R_{res} (PGLS $p<0.001$, $\lambda=0.763$, adjusted $r^2 = 0.109$; Figure 5a), while $acuity_{res}$ explains 16% of the variance in R_{res} (PGLS $p< 0.001$, $\lambda=0.790$, adjusted $r^2 = 0.138$; Figure 5b).

When agility category, activity pattern, and diet category are included as co-predictor variables in the best-fit PGLS model, none of these additional variables has a significant effect on R. Furthermore, inclusion of agility category and activity pattern increases the AICc value compared to the best-fit model (Table 3). Kruskal-Wallis tests comparing R_{res} values between agility category, activity pattern, and diet are also non-significant regardless of which model is used to calculate R_{res} (Table 5).

With axial eye diameters ranging between 0.9 and 2.0 mm, microphthalmic species have smaller eyes than the other species examined in this analysis (Table 1). Nonetheless, microphthalmic species have R values (0.6 - 1.7 mm) that overlap the lower end of the non-microphthalmic range (0.9 – 4.8 mm). When R is plotted against AD for the entire data set, all microphthalmic species fall above the regression line fit to the non-microphthalmic sample (Figure 6). A Wilcoxon rank-sum test shows that microphthalmic species have significantly larger residuals than and non-microphthalmic species ($W = 691$, p-value < 0.001).

Discussion

This study is the first comparative analysis of the influence of eye size and visual acuity on vestibular morphology in mammals. Semicircular canal radius of curvature has particular significance for interpreting interspecific variation in vestibular anatomy because canal R is a primary determinant of vestibular sensitivity to angular accelerations [18,50]. Because the semicircular canals play a critical role in gaze stabilization, we expected canal R to be positively correlated with both eye size and visual acuity. Our results confirm these expectations (Figure 3, Table 2) and demonstrate that mammals with larger eyes and higher visual acuity tend to have larger semicircular canal radii than mammals with smaller eyes and lower visual acuity. Our bivariate analyses also reveal that eye size has a greater influence on interspecific variation in canal R than does visual acuity. Compared to visual acuity, AD alone can explain about twice the variance in canal R (Table 2).

Given the findings of prior analyses [17,22,27,47], we also expected canal R, eye size, and visual acuity to be independently correlated with body mass. Our results confirm these expectations as well (Figure 4), and show that body mass alone explains a larger proportion of the variance in canal R than does either eye size or visual acuity (Table 2). Accordingly, we statistically controlled for the potentially confounding influence of body mass using PGLS multiple regression and PGLS partial regression models. Regardless of the method employed, these analyses are consistent in demonstrating that eye size and visual acuity have a significant effect on canal R that is independent of body mass or phylogenetic influence (Table 3, Figure 5). Indeed, our best-

fit PGLS multiple regression model shows that body mass, eye size, and visual acuity are all significant predictors of semicircular canal radius of curvature. Although body mass explains more than half of the interspecific variation in canal R according to this model, eye size and visual acuity nonetheless account for approximately a quarter and a tenth of this variation, respectively (Table 3). The best-fit multivariate analysis thus mirrors the results of our bivariate analyses in demonstrating that eye size has a greater influence on canal R than does visual acuity.

Because our findings support the conclusion that eye size and visual acuity independently influence semicircular canal radius of curvature, it is worth noting that these two predictor variables are functionally distinct. Although visual acuity tends to be greater in species with larger eyes[27], eye size has important consequences for many aspects of visual function. For example, having larger eyes may increase visual sensitivity if the light-gathering power of the dioptric apparatus is also increased [1,2]. Furthermore, eye size is only one of numerous factors (e.g., photoreceptor density, ganglion cell density, retinal summation, refractive errors, etc.) that determine a species' peak visual acuity [1,7,8,60]. In the context of our results, the fact that visual acuity remains significantly correlated with canal R in multiple regression models that also include AD probably reflects the important contribution of retinal anatomy in determining visual acuity. By this logic, eye size and visual acuity are not fully independent predictor variables, but some proportion of the interspecific variation in visual acuity unrelated to eye size is still a significant predictor of canal R.

Although diet and activity pattern are associated with interspecific differences in

eye morphology and visual acuity[1,2,22,37,71], these relationships do not translate into a significant independent influence of diet or activity pattern on canal R in our comparative sample (Tables 2 and 3). The failure of diet category and activity pattern to significantly influence R in our multiple regression models may reflect the fact that having AD and visual acuity as co-predictor variables already accounts for the relevant ecological differences between taxa. Furthermore, eye size and visual acuity both evolve in response to a variety of additional ecological factors (e.g., speed of locomotion [1,71-74] and constraints (e.g., head size, [7,23,75,76]).

Prior to this analysis, locomotor agility and body mass are the only two variables that have been suggested to directly influence semicircular canal radius of curvature [19]. Our data confirm a strong influence of body mass on canal R, and further suggest that body mass explains more of the interspecific variation in canal R than any other predictor variable (Tables 1-2). However, when we included the agility categories used by Spoor et al [19] as a predictor variable in our best-fit multiple regression model (along with BM, AD and visual acuity as co-predictors), agility category did not have a significant effect on canal R (Table 3). Including agility category in this model also increased the AICc value, indicating a weakening of the fit of the model. We also found that agility category had a non-significant influence on canal R when Kruskal-Wallis tests were used to compare the variation in canal size unexplained by both the best-fit model and the model including BM and AD as predictors (Table 5). Our results thus suggest that agility category [19] does not explain a significant proportion of the interspecific variation in

semicircular canal radius of curvature once the effects of body mass, eye size, and visual acuity are all taken into account. These findings may indicate that differences in eye size, visual acuity, and body mass between the species in our comparative sample already account for variation in canal R associated with locomotion. Indeed, maximum running speed is currently the best-known predictor of eye size other than body mass [74]. However, our non-significant results for agility may also be due to the fact that agility categories were qualitatively assessed [19], and it is currently unclear how such categories relate to the angular head accelerations that are actually detected by the semicircular canals during locomotion. At present, measurements of the head accelerations that mammal species experience during locomotion are only available for a small number of species [18,77], thus limiting options for comparative study of the influence of locomotor kinetics on vestibular morphology.

Although our analyses provide strong evidence for an influence of both eye size and visual acuity on semicircular canal radius of curvature, our data for microphthalmic species serve as a reminder that visual factors are not the only selective influence on canal R. Indeed, the microphthalmic taxa sampled in this study have canal radii that are significantly larger than would be predicted based on their eye size alone (Figure 6). In these species, the evolution of extremely reduced eyes was not accompanied by comparable degrees of reduction in canal R, suggesting that some minimum level of semicircular canal sensitivity that must be maintained even if gaze stabilization is not required. This finding reinforces the fact that, although gaze stabilization is a major

function of the semicircular canals, semicircular canal output is useful in other contexts such as self-motion perception, postural control, and perception of the body in space [78-80]. These other demands on the vestibular system presumably provide selective pressure for most microphthalmic species to maintain semicircular canals with radii of curvature that are comparable to species with much larger eyes.

These results lead us to suggest an evolutionary scenario to account for the observed interspecific relationships among eye size, visual acuity, and semicircular canal radius of curvature in mammals (Figure 7). Eye size and visual acuity are hypothesized to increase in an evolutionary lineage due to multiple selective factors, such as an increased speed of locomotion [51] or visually predatory habits [22]. Regardless of the ecological context, selection for larger eyes and increased acuity creates a functional demand for more precise gaze stabilization to maintain image fixation and proper visual function. Meeting this demand requires increased vestibular sensitivity, which in turn may be achieved through increases in canal radius of curvature [13-18]. Thus, the evolution of larger eyes and greater visual acuity leads to selection for larger canal radii and a pattern of correlated evolution in these traits (Figure 7). However, not all variation in canal R is attributable to visual factors, as is demonstrated by the persistence of semicircular canals following the evolutionary loss of functional eyes. Though we found no effect of locomotor agility on canal R after accounting for eye size, visual acuity, and body mass, we nonetheless expect locomotion to exert a major selective influence on canal R because locomotion generates angular head accelerations, and visual fixation cannot be maintained during locomotion without vestibular feedback [4,77]. Locomotion may

influence R size via the relationship between maximum speed and eye size [74] (Figure 7) or other aspects of canal morphology (i.e. orthogonality) more directly [77].

Appendix

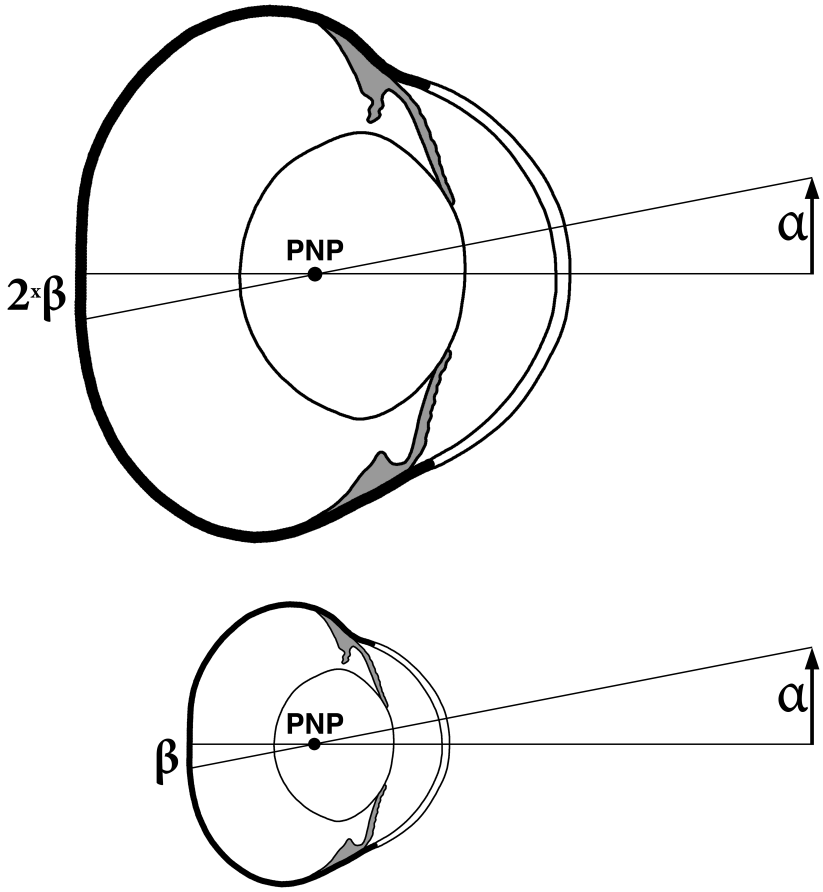

Figure 1. Effect of eye size on absolute displacement of the retinal image due to uncorrected head movements. In this schematic example, two eyes have identical shape but differ in axial diameter; here the larger eye has an axial diameter approximately twice that of the smaller eye. Both eyes are positioned so that a point target is the same distance from the posterior nodal point (PNP; position approximate). Uncorrected head movements cause the relative position of the point source in object space to to shift (arrow) by the same magnitude (α) for each eye. This relative shift in the location of the visual target leads to a shift in retinal image position in the larger eye (2 x β) that is twice the magnitude of the shift in retinal image position in the smaller eye (β).

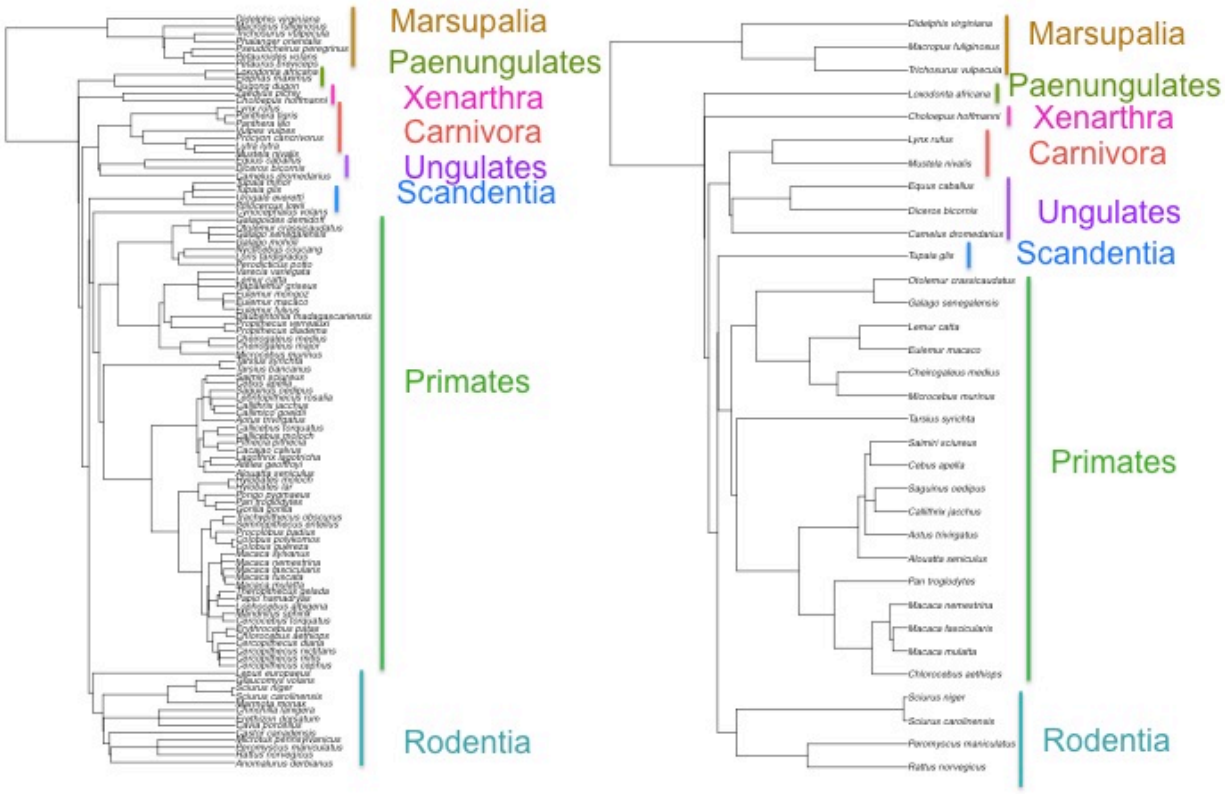

Figure 2. Phylogeny of species included in comparative datasets. a) Species for which R and axial eye diameter values were available and included in the full dataset. b) Subset of species in a) for which acuity data was also available.

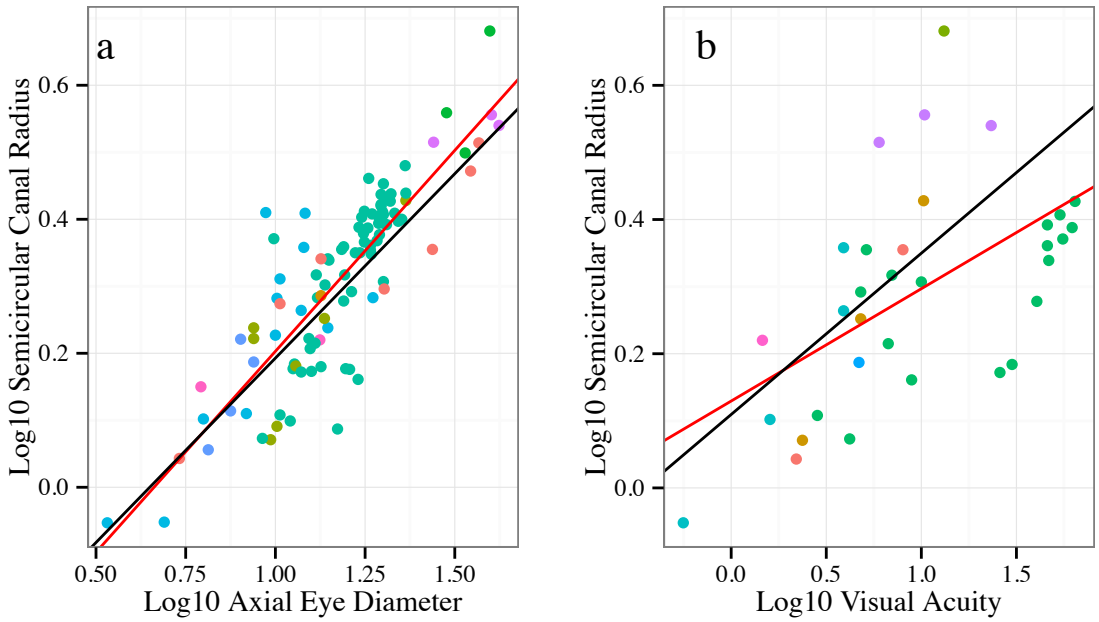

Figure 3. A significant portion of interspecific variation in semicircular canal R is explained by variation in both eye size and visual acuity. Hashed lines represent OLS regressions and solid lines represent PGLS regressions. Data point colors represent supraordinal taxonomic affiliation (see Figure 2 for key).

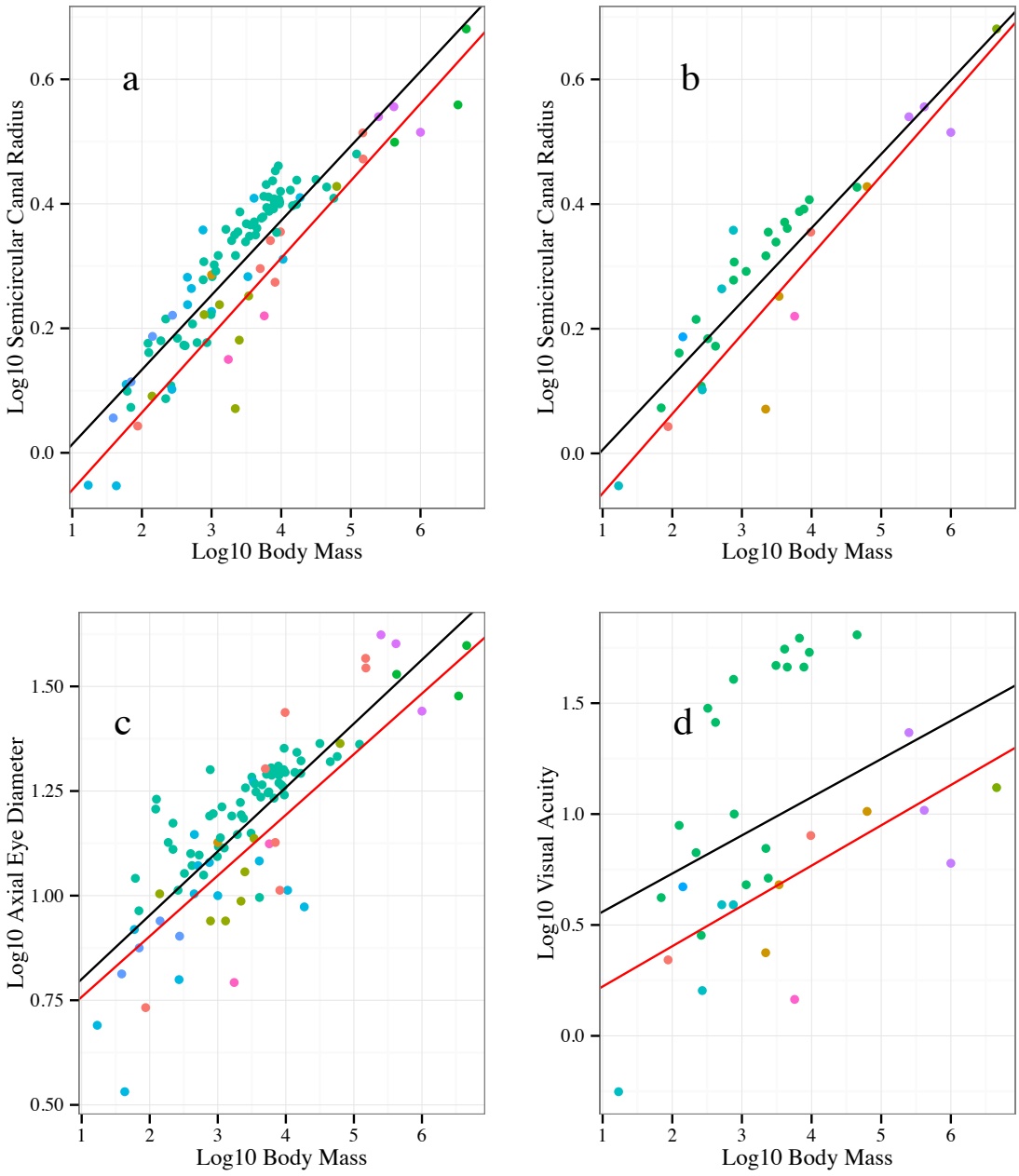

Figure 4. Body mass is significantly correlated with all three variables of interest. The regressions in a) and c) are based on the entire sample while the regressions in b) and d) are based on the subset of species for which acuity data were available. Hashed lines represent OLS regressions and solid lines represent PGLS regressions. Data point colors represent supraordinal taxanomic affiliation (see Figure 2 for key).

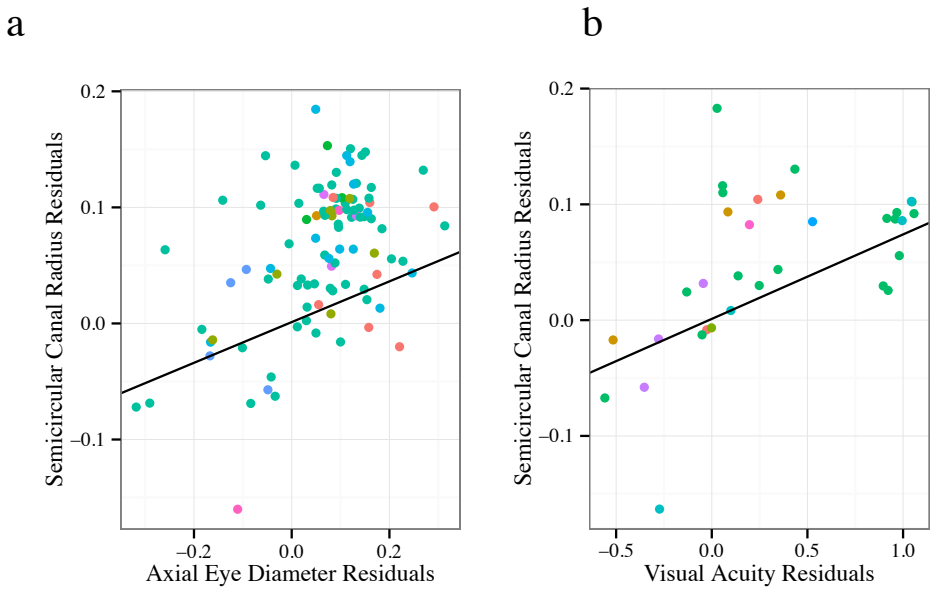

Figure 5. Eye size (a) and acuity (b) remain positively correlated when the effect of body mass is held constant using residuals. Lines represent PGLS regressions. Data point colors represent supraordinal taxanomic affiliation (see Figure 2 for key).

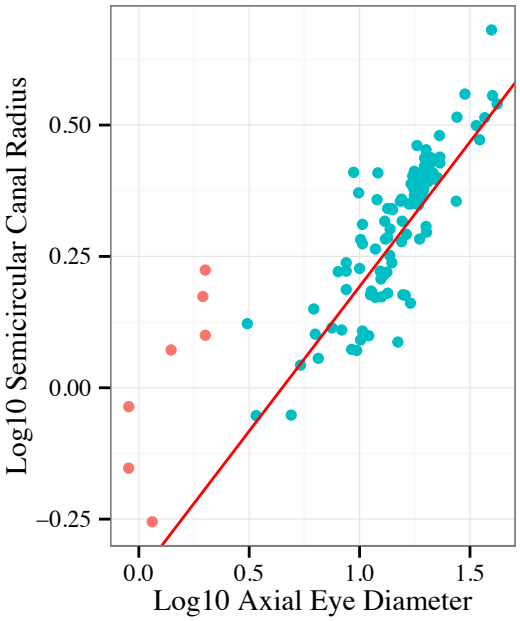

Figure 6. Microphthalmic taxa (in pink) exhibit a range of semicircular canal R that overlaps with R values for species with significantly larger eyes (in blue). Red line represents PGLS regression for non-mircophthalmic taxa.

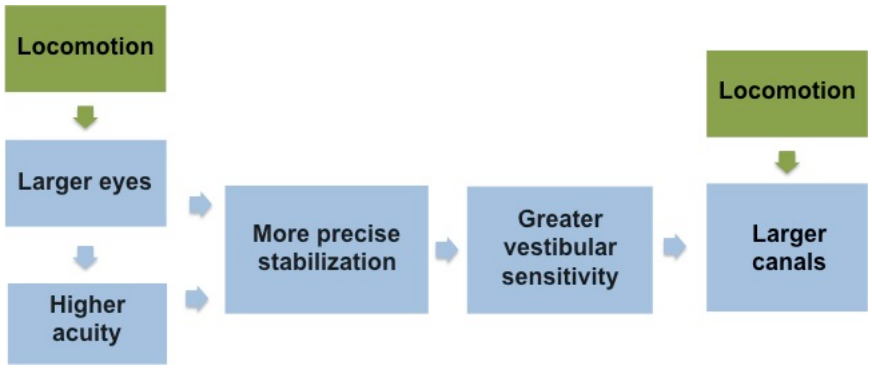

Figure 7. Hypothesized selective relationships between eye size, visual acuity, canal size and locomotion.

Order	Species	BM, g	R, mm	AD, mm	Acuity, c/deg	Agility score	Activity pattern	Diet	Source
Afrosorcida	*Hemicentetes semispinosus**	120	1.7	2	-	-	-	-	-,-
Artiodactyla	*Camelus dromedarius*	415000	3.6	40	10.4	4	D	H	24,48
Artiodactyla	*Gazella bennetti*	23000	2.6	8.5	-	4	D	-	-,-
Artiodactyla	*Oryx beisa (gazella)*	198625	2.9	37.1	-	4	C	-	-,-
Carnivora	*Felis catus*	3601	1.8	27.4	-	4	C	-	-,-
Carnivora	*Lutra lutra*	8175	1.9	10.3	-	5	C	AP	-,-
Carnivora	*Lynx rufus*	9750	2.3	27.4	8	4	C	AP	25,49
Carnivora	*Mustela nivalis*	87	1.1	5.4	2.2	4	C	AP	26,49
Carnivora	*Panthera leo*	148750	3.3	36.9	-	4	C	AP	-,49
Carnivora	*Panthera tigris*	150100	3	35	-	4	C	AP	-,49
Carnivora	*Procyon cancrivorus*	6994	2.2	13.4	-	3	C	AP	-,49
Carnivora	*Vulpes vulpes*	5000	2	20.1	-	4	N	-	-,-
Dermoptera	*Cynocephalus volans*	1000	1.9	13.4	-	6	N	-	-,-
Didelphimorphia	*Didelphis virginiana*	2195	1.2	9.7	2.4	2	N	-	27,-
Diprotodontia	*Macropus fuliginosus*	62633	2.7	23.1	10.3	6	C	-	27,-
Diprotodontia	*Petauroides volans*	1300	1.7	8.7	-	6	N	-	-,-
Diprotodontia	*Petaurus breviceps*	140	1.2	10.1	-	6	N	-	-,-
Diprotodontia	*Phalanger orientalis*	2500	1.5	11.4	-	2	N	-	-,-
Diprotodontia	*Pseudocheirus peregrinus*	781	1.7	8.7	-	4	N	-	-,-
Diprotodontia	*Trichosurus vulpecula*	3410	1.8	13.7	4.8	4	N	-	28,-

Table 1. Raw data used in analyses. Where possible, data points represent species means. BM - body mass; AD - axial eye diameter; R - mean semicircular canal radius of curvature; c/deg- cycles per degree; -, data not available; C- cathemeral; D- diurnal; N- nocturnal; H- herbivore; AP- active predator. Listed sources are for acuity and diet, all other sources are listed in the text. * Microphthalmic species † Acuity data was not reported for the species for which R values were published; data from a congener not significantly different in mass was used. Species with published acuity values matched at congeneric level were: *Alouatta caraya*, *Choloepus didactylus* and *Saguinus midas*.

Lagomorpha	*Lepus europaeus*	3330	1.9	18.7	-	5	C	-	-,-
Paucituberculata	*Caenolestes fuliginosus**	25	1.5	1.9	-	3	-	-	-,-
Perissodactyla	*Diceros bicornis*	1000000	3.3	27.6	6	4	C	H	29,48
Perissodactyla	*Equus caballus*	250000	3.5	42	23.3	4	C	H	30,48
Primates	*Alouatta seniculus*	6700	2.4	17.1	62.1	2	D	H	27,48
Primates	*Aotus trivirgatus*	775	2	20	10	5	N	-	32,-
Primates	*Ateles geoffroyi*	7535	2.7	19.7	-	4	D	-	-,-
Primates	*Cacajao calvus*	3165	2.3	19.2	-	4	D	-	-,-
Primates	*Callicebus moloch*	1020	1.9	13.1	-	4	D	-	-,-
Primates	*Callicebus torquatus*	1245	2.1	13	-	4	D	-	-,-
Primates	*Callimico goeldi*	533	1.6	12.5	-	5	D	-	-,-
Primates	*Callithrix jacchus*	324	1.5	11.3	30	6	D	-	31,-
Primates	*Cebus apella*	3085	2.2	14.1	46.8	4	D	-	33,-
Primates	*Cercocebus torquatus*	6200	2.5	19.4	-	6	D	-	-,-
Primates	*Cercopithecus cephus*	4290	2.2	17.2	-	4	D	-	-,-
Primates	*Cercopithecus diana*	5200	2.4	19.5	-	6	D	-	-,-
Primates	*Cercopithecus mitis*	7930	2.5	19.4	-	4	D	-	-,-
Primates	*Cercopithecus nictitans*	5465	2.4	17.6	-	4	D	-	-,-
Primates	*Cheirogaleus major*	400	1.5	12.6	-	4	N	-	-,-
Primates	*Cheirogaleus medius*	261	1.3	10.3	2.8	4	N	-	37,-
Primates	*Chlorocebus aethiops*	4099	2.3	9.9	55.4	4	N	H	27,48
Primates	*Colobus guereza*	9774	2.6	19.7	-	5	D	-	-,-
Primates	*Colobus polykomos*	9100	2.9	18.2	-	4	D	-	-,-
Primates	*Daubentonia madagascariensis*	2555	2.4	18.1	-	6	N	-	-,-
Primates	*Erythrocebus patas*	9450	2.5	22.5	-	6	D	-	-,-
Primates	*Eulemur fulvus ssp.*	2146	2.2	16.7	-	4	C	-	-,-
Primates	*Eulemur macaco*	2389	2.3	15.3	5.1	4	C	H	37,48
Primates	*Eulemur mongoz*	1606	2.3	15.5	-	4	C	-	-,-
Primates	*Galago moholi*	187	1.5	13.4	-	6	N	-	-,-
Primates	*Galago senegalensis*	220	1.6	12.9	6.7	6	N	AP	40,48
Primates	*Galagoides demidoff*	62	1.3	11	-	4	N	-	-,-
Primates	*Gorilla gorilla*	120950	3	23	-	2	D	-	-,-

Table 1, *continued*.

Primates	*Hapalemur griseus*	1091	2	13.8	-	4	D	-	-,-
Primates	*Hylobates lar*	5620	2.6	17.7	-	6	D	-	-,-
Primates	*Hylobates moloch*	6580	2.6	19.9	-	6	D	-	-,-
Primates	*Lagothrix lagotricha*	7367	2.5	20	-	3	D	-	-,-
Primates	*Lemur catta*	2210	2.1	15.6	7	4	D	-	41,-
Primates	*Leontopithecus rosalia*	620	1.5	11.2	-	6	D	-	-,-
Primates	*Lophocebus albigena*	8250	2.8	20	-	5	D	-	-,-
Primates	*Loris tardigradus*	220	1.2	14.9	-	2	N	-	-,-
Primates	*Macaca fascicularis*	4475	2.3	18.4	46	4	D	-	35,-
Primates	*Macaca fuscata*	9515	2.5	17.4	-	4	D	-	-,-
Primates	*Macaca mulatta*	9286	2.6	20	53.6	4	D	-	34,-
Primates	*Macaca nemestrina*	7771	2.5	20.4	46	4	D	-	35,-
Primates	*Macaca sylvanus*	13550	2.6	19.7	-	4	D	-	-,-
Primates	*Mandrillus sphinx*	31600	2.8	23.1	-	4	D	-	-,-
Primates	*Microcebus murinus*	69	1.2	9.2	4.2	4	N	AP	36,48
Primates	*Nycticebus coucang*	856	1.5	15.7	-	2	N	-	-,-
Primates	*Otolemur crassicaudatus*	1150	2	16.3	4.8	4	N	-	38,-
Primates	*Pan troglodytes*	44967	2.7	20.9	64.3	4	D	-	39,-
Primates	*Papio hamadryas*	16730	2.7	21	-	4	D	-	-,-
Primates	*Perodicticus potto*	985	1.7	12.4	-	2	N	-	-,-
Primates	*Pithecia pithecia*	1940	2.2	14	-	4	D	-	-,-
Primates	*Pongo pygmaeus*	56950	2.6	21.5	-	2	D	-	-,-
Primates	*Procolobus badius*	8583	2.3	18.4	-	4	D	-	-,-
Primates	*Propithecus diadema*	6100	2.7	20.2	-	6	D	H	-,48
Primates	*Propithecus verreauxi*	3643	2.3	17.7	-	6	D	H	-,48
Primates	*Saguinus oedipus*	418	1.5	11.8	25.9	6	D	-	27,-
Primates	*Saimiri sciureus*	759	1.9	15.5	40.5	6	D	-	34,-
Primates	*Semnopithecus entellus*	14533	2.5	22	-	4	D	-	-,-
Primates	*Tarsius bancanus*	123	1.5	16.1	-	6	N	AP	-,48
Primates	*Tarsius syrichta*	126	1.4	17	8.9	6	N	AP	37,48
Primates	*Theropithecus gelada*	16567	2.5	19.6	-	4	D	-	-,-
Primates	*Trachypithecus obscurus*	7900	2.6	18.6	-	4	D	-	-,-
Primates	*Varecia variegata*	3508	2.2	18.5	-	4	D	-	-,-
Proboscidea	*Elephas maximus*	3450000	3.6	30	-	3	C	H	-,48
Proboscidea	*Loxodonta africana*	4540000	4.8	39.6	13.2	3	C	H	44,48

Table 1, *continued*.

Rodentia	*Anomalurus derbianus*	453	1.7	14	-	6	N	-	-,-
Rodentia	*Castor canadensis*	18667	2.6	9.4	-	4	C	-	-,-
Rodentia	*Cavia porcellus*	1000	1.7	10	-	4	C	-	-,-
Rodentia	*Chinchilla laniger*	450	1.9	10.1	-	6	C	-	-,-
Rodentia	*Cryptomys mechowi**	400	1.3	2	-	2	-	-	-,-
Rodentia	*Erethizon dorsatum*	10623	2	10.3	-	2	C	-	-,-
Rodentia	*Glaucomys volans*	59	1.3	8.3	-	6	N	-	-,-
Rodentia	*Marmota monax*	4075	2.6	12.1	-	4	D	-	-,-
Rodentia	*Microtus pennsylvanicus*	43	0.9	3.4	-	4	C	-	-,-
Rodentia	*Peromyscus maniculatus*	17	0.9	4.9	0.6	4	N	-	43,-
Rodentia	*Rattus norvegicus*	270	1.3	6.3	1.6	4	N	-	42,-
Rodentia	*Sciurus carolinensis*	514	1.8	11.8	3.9	6	D	-	45,-
Rodentia	*Sciurus niger*	754	2.3	12	3.9	6	D	-	45,-
Scandentia	*Ptilocercus lowii*	39	1.1	6.5	-	4	N	-	-,-
Scandentia	*Tupaia glis*	142	1.5	8.7	4.7	4	D	-	46,-
Scandentia	*Tupaia minor*	70	1.3	7.5	-	4	D	-	-,-
Scandentia	*Urogale everetti*	275	1.7	8	-	4	D	-	-,-
Sirenia	*Dugong dugon (Halicore australis)*	425000	3.2	33.8	-	1	C	-	-,-
Sorciomorpha	*Blarina brevicauda**	16	0.7	0.9	-	4	-	-	-,-
Sorciomorpha	*Scalopus aquaticus**	81	0.9	0.9	-	2	-	-	-,-
Sorciomorpha	*Sorex cinereus**	4	0.6	1.1	-	4	-	-	-,-
Sorciomorpha	*Talpa europaea**	97	1.2	1.4	-	4	-	-	-,-
Xenarthra	*Choloepus hoffmanni*	5720	1.7	13.3	1.5	1	N	-	27,-
Xenarthra	*Zaedyus pichiy*	1740	1.4	6.2	-	3	C	-	-,-

Table 1, *continued*.

Variables	n	Model	Slope	y-intercept	p-value	Adjusted r^2	ϱ	λ
$\log_{10}$ R (y), $\log_{10}$ AD (x)	104	OLS	0.599	-0.396	< 0.001	0.724	0.829	-
	104	PGLS	0.550	-0.358	< 0.001	0.580	-	0.896
$\log_{10}$ R (y), $\log_{10}$ acuity (x)	33	OLS	0.167	0.129	<0.001	0.297	0.640	-
	33	PGLS	0.240	0.110	<0.005	0.338	-	0.930
$\log_{10}$ R (y), $\log_{10}$ BM (x)	104	OLS	0.120	-0.106	< 0.001	0.807	0.902	-
	104	PGLS	0.124	-0.183	< 0.001	0.763	-	0.938
$\log_{10}$ AD (y), $\log_{10}$ BM (x)	104	OLS	0.152	0.648	< 0.001	0.647	0.792	-
	104	PGLS	0.145	0.612	< 0.001	0.533	-	0.935
$\log_{10}$ acuity (y), $\log_{10}$ BM (x)	33	OLS	0.172	0.386	<0.05	0.1254	0.524	-
	33	PGLS	0.182	0.041	<0.001	0.247	-	0.982

Table 2. Bivariate regressions. ϱ, Spearman's rho; λ, Pagel's lambda; -, not applicable.

Predictor variables	n*	p-value	λ	Adjusted r^2	AICc	Variable	Coef	p-value	Partial r^2
BM AD	33	< 0.001	0.826	0.873	-97.052	BM	0.093	< 0.001	0.647
						AD	0.213	< 0.01	0.266
BM Acuity	33	< 0.001	0.785	0.868	-95.112	BM	0.113	< 0.001	0.785
						Acuity	0.073	< 0.05	0.140
AD Acuity	33	< 0.001	0.561	0.784	-75.792	AD	0.544	< 0.001	0.679
						Acuity	0.076	< 0.05	0.145
BM AD Acuity	33	< 0.001	0.758	0.890	-99.091	BM	0.085	< 0.001	0.591
						AD	0.190	< 0.05	0.237
						Acuity	0.059	< 0.05	0.113
BM AD Acuity Agility	33	< 0.001	0.662	0.897	-98.153	BM	0.093	< 0.001	0.647
						AD	0.161	< 0.05	0.201
						Acuity	0.051	n.s.	
						Agility	0.083	n.s.	
BM AD Acuity Activity	33	< 0.001	0.657	0.881	-97.009	BM	0.063	< 0.001	0.440
						AD	0.292	<0.005	0.364
						Acuity	0.009	n.s.	
						Activity CvD	0.007	n.s.	
						Activity CvN	0.011	n.s.	
						Acitvity DvN	0.012	n.s.	
BM AD Diet	20	< 0.001	0.645	0.090	-93.374	BM	0.067	< 0.001	0.552
						AD	0.308	<0.005	0.382
						Diet	0.037	n.s.	

Table 3. Multivariate PGLS models of R. Partial r^2 values only reported for significant variables. λ, Pagel's lambda [57]; AICc, Akaike Information Criterion (corrected for relatively small sample size); Coef, correlation coefficient ; CvD; cathemeral vs. diurnal; CvN, cathemeral vs. nocturnal; DvN, diurnal vs. nocturnal. * Restricted sample sized used to permit meaningful model comparisons.

Predictor variables	n	p-value	λ	Adjusted r^2	AIC	AICc
BM AD	33	< 0.001	0.826	0.873	-97.88	-97.06
BM AD BM:AD	33	< 0.001	0.834	0.873	-97.05	-96.23
BM Acuity	33	< 0.001	0.785	0.868	-95.94	-95.11
BM Acuity BM:Acuity	33	< 0.001	0.893	0.832	-89.26	-88.44
AD Acuity	33	< 0.001	0.561	0.784	-76.62	-75.79
AD Acuity AD:Acuity	33	< 0.001	0.561	0.778	-74.07	-73.25
Body mass AD Acuity	33	< 0.001	0.758	0.89	-100.52	-99.091
Body mass AD Acuity BM:AD	33	< 0.001	0.828	0.869	-95.22	-92.99

Table 4. Regression statistics, with and without interaction terms. Interaction terms indicated using colons.

Variable	R_{res} from best fit model		R_{res} from two-predictor model	
	p-value	n	p-value	n
Agility	0.551	33	0.941	109
Diet	0.575	12	0.510	20
Activity	0.054	33	0.993	104

Table 5. Kruskal Wallis statistics. Best-fit model predictor variables include body mass, axial eye diameter and visual acuity; two predictor model includes body mass and axial eye diameter.

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